# THE MORPHOLOGY AND GENERIC RELATIONSHIPS OF SOME FISSIPAROUS HETERONEMERTINES

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*Abstract.* — No morphological difference could be found between a fissiparous heteronemertine from New Zealand and other fissiparous species with similar external appearances. All constitute a single species. Significant anatomical characters are shared with *Lineus lacteus* (Rathke, 1843) and *L. pseudolacteus* Gontcharoff, 1951. The genus *Myoisophagos* is erected to contain the three species with *M. sanguineus* (Rathke, 1799) designated as type species. Significant morphological characters separate the new genus from the genus *Lineus*.

Clumps of slender nemertines were encountered beneath rocks on the reef just seaward of the rubble beach along the outer face of the Kaikoura Peninsula, New Zealand during the early months of 1983 and 1986. The clusters were reminiscent of *Lineus socialis* (Leidy, 1855) from New England midtidal rocky shores as was the pigmentation and rather regularly spaced annuli behind the head region of the body to that of the New England species. Five specimens of comparable size were bisected, one at the first annulus and the others successively one annulus further back to determine if the animals could regenerate. The heads were retained in a single jar, and each of the posterior pieces was placed in a separate jar of sea water maintained on a sea water table. Two days later, the posterior pieces had fragmented; with most of the fragments bearing one or two annuli, rarely three. Fourteen days after fission, the fragments had developed white heads with two red eyes. Existing descriptions of fissiparous lineid species contain no anatomical data by which species can be identified. Living specimens of "species" to which names had been assigned were obtained and a morphological comparison was undertaken.

## Materials and Methods

In addition to the specimens from Kaikoura, New Zealand, living specimens of *Lineus lacteus* (Rathke, 1843), *L. pseudolacteus* Gontcharoff, 1951, *L. sanguineus* (Rathke, 1799), and *L. nigricans* Bürger, 1892 were obtained from the colonies maintained by Prof. J. Bierne. Living specimens of *L. vegetus* Coe, 1931 were furnished by Prof. P. Roe from central California rocky beaches, and *L. socialis* (Leidy, 1855) was collected from a number of rocky shoreline outcroppings between Nahant, Massachusetts and Georgetown, Maine. Anesthetization, fixation, sectioning, and staining were as described in Riser (1988).

## Systematic Account

### Lineidae *sensu* Gibson, 1982
### *Myoisophagos,* new genus

*Type species.* — *Myoisophagos sanguineus* (Rathke, 1799), new combination.
*Diagnosis.* — With three apical sensory organs; frontal glands absent; rhynchodaeum attached ventrally and thus with a single cephalic blood lacuna arched over the rhynchodaeum; rhynchocoel muscle layers not interwoven nor interwoven with muscles of body wall; proboscis with two muscle layers, inner longitudinal and outer circular; vascular plexus in foregut region; neurochord cells and caudal cirrus absent; subepidermal gland cells penetrate OLM, some contact medullary nerve plexus; with subepithelial esophageal gland cells and longi-

tudinal muscles; longitudinal muscle plate between rhynchocoel and foregut absent; radial muscles to either side of the rhynchocoel pass beneath the rhynchocoel crossing to the opposite side and continue around the foregut.

*Etymology.*—*myos* Gr. muscular, *oisophagos* Gr. esophagus.

Radial muscles from the body wall arboresce through the subepithelial esophageal gland layer (Figs. 8, 11). They, with the subepithelial esophageal longitudinal muscles control expansion and contraction of the foregut. The dorsal radial muscles form a sling around the rhynchocoel (Fig. 11) crossing beneath that organ and continuing around the foregut as circular bands. These bands lie amidst the bases of the esophageal glands of the empty foregut (Fig. 8), but are pressed closer to the subepithelial longitudinal muscles of the inflated organ. Friedrich (1935) referred to these radial fibers in the foregut region as dorsoventral muscles.

Bürger (1897–1907; table 3, fig. 18) illustrated the penetration of the sub-epidermal glands to the ICM, as later described by Coe (1931).

*Myoisophagos sanguineus* (Rathke, 1799), new combination
Figs. 5, 8–11

*Planaria sanguinea* Rathke, 1799:83.
*Lineus sanguineus* McIntosh, 1873–1874: 188–190. auctt.
*Lineus nigricans* Bürger, 1892:159. auctt. not *L. nigricans* Isler 1901, 1902.
*Nemertes socialis* Leidy, 1855:143; Verrill, 1873:324, 392, 628.
*Lineus socialis* Verrill 1892:424–425. auctt.
*Lineus ruber, forme β* Oxner 1909, 1910; Nusbaum & Oxner, 1910a, 1910b. not *Lineus ruber* (Müller, 1771).
*Lineus vegetus* Coe, 1931:54–60. auctt.

*Species diagnosis.*—Gliding individuals may attain 20 cm in length and 1.2 mm diameter. Brain region red, body of small individuals (less than 15 mm long) transparent white or cream color, larger specimens vary from greyish green to brownish black or red. Three to seven ocelli in dorsal wall of cephalic fissures on each side, occasionally the same number on both sides. Anterior end of buccal cavity close to posterior ends of cerebral organs. Subepidermal glands do not penetrate the inner circular muscles. Subepidermal longitudinal muscle bundles are almost as large (Fig. 11) as the bundles of the OLM. Ganglion layer of brain enclosed with connective tissue (Fig. 4). Excretory system usually with a short segment in dorsal wall of right preoral blood lacuna. Sexual reproduction abortive, oocytes aberrant, fissiparous. Contract by spiral coiling.

Dr. Janet Moore generously recorded length versus color and ocelli number of living specimens at Kaikoura. She noted that individuals under 20 mm, "slightly extended," were white with three ocelli on each side; specimens from 25–35 mm were red with 3–6 ocelli per side, and beyond that were "very dark" with 5–7 eyes on each side. This corresponds with personal observations of individuals in the Gulf of Maine and with regenerating fragments of the other "species." Specimens collected from mussel beds on exposed cliff faces at Nahant are frequently bright red while those beneath rocks on the nearby reef vary much like the New Zealand individuals. Riser (1993) noted that in culture all of these "species" were indistinguishable by color when fed a diet of *Mytillus/Buccinum* gonad/digestive gland. The uroporphyrin pigment (Vernet & Bierne 1983, Vernet 1983) diminishes in regenerating fragments, and the very small and widely scattered pigment granules are not readily evident in histological preparations of regenerates that have not begun feeding. Regenerating individuals usually pass through a color phase similar to figure 12 in the description of *Lineus flammeus* Monastero, 1930. The closeness of the buccal cavity to the cerebral organs is obvious in living animals.

Preoral contraction may alter the shape of the mouth from elongate to round; draw
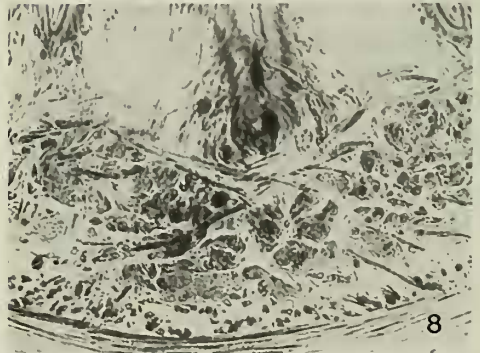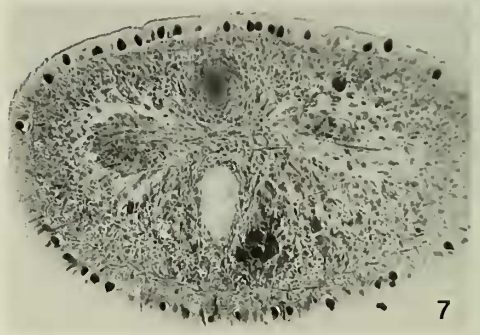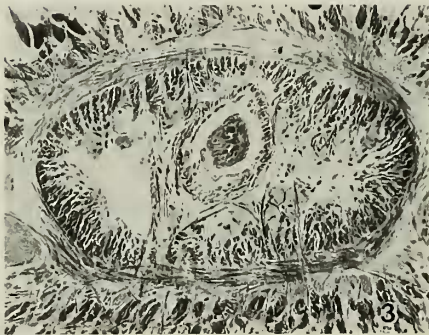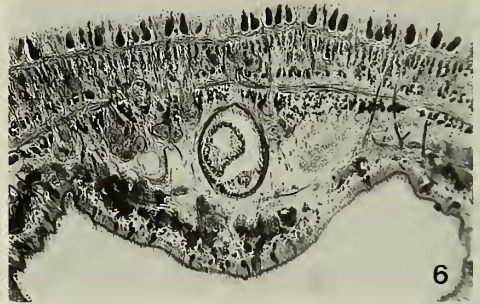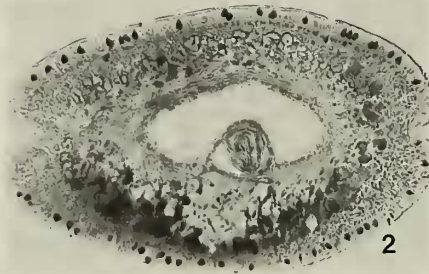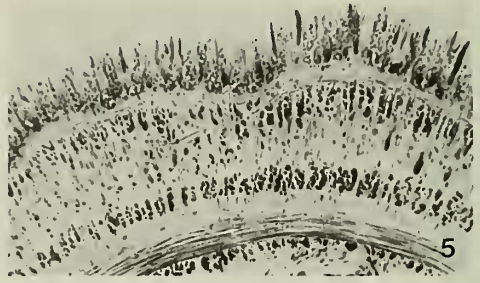
Figs. 1–8.   1–4, 7, *Myoisophagos lacteus*; 1, longitudinal section in preoral region packed with parenchymatous connective tissue; 2, cross section near anterior end with ventral parenchymatous tissue, serous glands, and pale (grey) mucus glands; 3, pre-oral, postcerebral cross section through rhynchocoel, and paired cerebral lacunae; 4, cross section through brain with ganglion cells enclosed by connective tissue; 5, *M. sanguineus,* cross section through dorsal body wall; 6, *M. pseudolacteus,* cross section near posterior end of mouth; 7, cross section near rhynchodaeal pore, three apical sensory organs not cut in common plane; 8, *M. sanguineus,* cross section through ventral body wall of foregut region.

the cerebral organs posteriorly to proximate the buccal cavity; and alter the location of post cerebral as well as periforegut organs. Coe (1951b) noted the unique presence of the preoral segment of the excretory system and that it was not connected to the postoral portion, however he mistook the anterior end of the system on the left side to be the posterior end of a preoral segment. Figures 19 and 20 of Corrêa (1956) clearly show the two systems with the efferent duct at the anterior end of the left side exiting in the midoral region. The efferent duct is at the posterior end of the preoral segment and exits on the dorsolateral surface of the body near the anterior end of the mouth. It is not connected with the remainder of the system which begins near the middle of the mouth. In the present study, three or more efferent ducts were routinely encountered on each side in addition to the duct from the preoral system of the one side. Oudemans (1885) noted that the excretory system of his "greatly contracted" specimens did not "reach the mouth" anteriorly, and that the number of efferent ducts appeared to be related to the "growth and age" of the individual. Coe (1931) reported the presence of "several pairs" of "efferent ducts" in *L. vegetus* and one specimen, with five on one side and six on the other. (The type specimens of *L. vegetus* have disappeared and the only slides that he deposited with the Peabody Museum at Yale University are labeled "for anatomical study." The sections are shrunken and folded so that very little information can be obtained from them.) Of the twenty seven anterior ends of specimens sectioned in the present study, one (*socialis*) lacked the preoral segment of the system. Moretto et al. (1976) did not mention a preoral segment in their account and figured three efferent ducts on each side. Cyrtocytes occur in clumps at the anterior ends of both excretory segments, most obviously projecting from the rhynchocoel wall (Fig. 10) but also in scattered clumps along the dorsal and lateral walls of the blood lacunae.
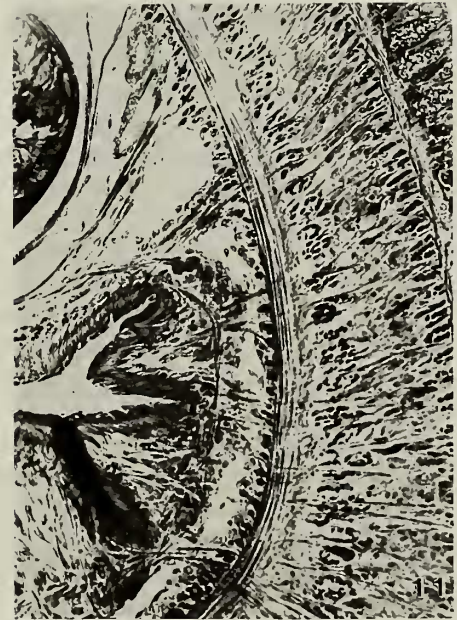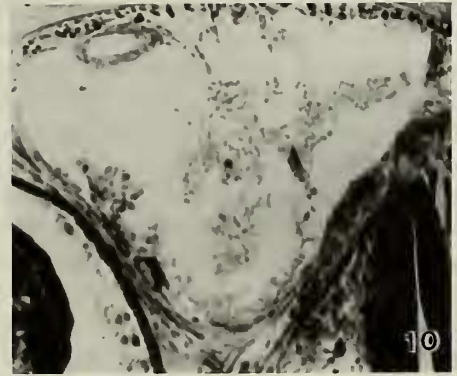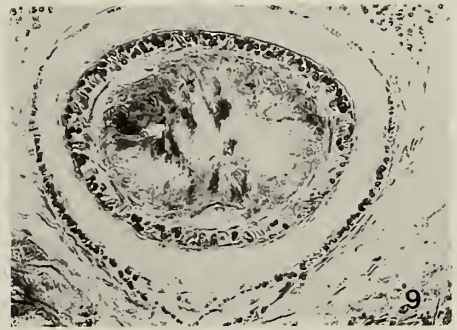


Figs. 9–11.  *Myoisophagos sanguineus*; 9, cross section through anterior proboscis; 10, cross section through anterior oral region with cyrtocytes on rhynchocoel wall; 11, cross section through posterior oral region with radial muscles forming sling and circular bands.

Differential contraction of the muscles can be seen in cross sections in which the subepidermal longitudinal muscle bundles appear to be duplicated with a spiral fiber from the subepidermal circular muscles dividing the bundles (Fig. 5).

Coe (1899) stated that the eggs of *L. socialis* matured in "mid-winter" and sometimes were "deposited in captivity in masses of mucus" where they developed "readily at least to the stage of swimming gastrulae." In 1943, he listed *L. socialis* as an abundant species which furnished "excellent material for the study of normal and experimental embryology" and, without elaboration, stated that "some individuals reproduce sexually during the autumn and early spring." McIntosh (1873–1874) reported that the eggs of *L. sanguineus* matured in October but did not mention spawning. Gontcharoff (1951) noted the presence of gonopores in the males of *M. sanguineus* and a single observation of the shedding of sperm. She noted that female gonoducts rarely could be found penetrating the epidermis; oocytes were few in number; spawning did not occur in culture, nor when freshly collected specimens were paired in vitro. She tentatively concluded that oogenesis was abortive, and that propagation of the species was by asexual reproduction. She noted absorption of oocytes, and their occasional occurrence in the intestine. The ovaries of some females collected at Nahant in April and May contained oocytes which had undergone autolysis, with only the nucleolus, nuclear membrane and much wrinkled cell membrane distinguishable. Degeneration of the nearby wall of the intestine as reported by Gontcharoff, sometimes was apparent, although oocytes were not encountered in the lumen of the gut. "Normal oocyte development" was reported for *L. sanguineus* from Uruguay by Bierne (1983), [recorded as *L. socialis* in Bierne et al. (1993)]. Oocyte production and sexual reproduction are not synonymous and references to the latter event are questionable, but, genetic evidence (Alex Rogers, pers. comm.) suggests that some sexual reproduction occurs in this species.

Coe (1951) noted that the fauna of southern Florida was tropical and that boreal species such as *L. socialis* were restricted to the northern Gulf of Mexico and northern coast of Florida on the Atlantic side. J. Norenburg (pers. comm.) observed "*L. socialis*" with "mature ova" along the Indian River near Fort Pierce, Florida in January. The identification by Corrêa (1961) of *L. socialis* from the Virgin Islands based upon the appearance of the head of a "preserved fragment" is suspect. Isler (1901, 1902) recorded *L. nigricans* from Punta Arenas, Chile among the preserved specimens collected by Plate, but furnished no data to support the identification. His slides are of an unknown species which does not conform to *Lineus* nor to *Myoisophagos*. *M. sanguineus* is a temperate-water intertidal species that is tolerant of gradual salinity and thermal changes. Under adverse conditions, individuals undergo fragmentation and some of the fragments may encyst. Verrill (1873) listed *Nemertes socialis* among "species commonly found on piles and timbers of wharves and bridges on buoys, bottoms of vessels, and other submerged wood-work." The biology of *M. sanguineus* would allow for transport in the fouling community on ships and account for the wide distribution of the species in temperate waters.

*Myoisophagos pseudolacteus*
(Gontcharoff, 1951), new combination
Fig. 6

*Lineus pseudolacteus* Gontcharoff, 1951:157 auctt.
*Lineus sanguineus pseudolacteus* Bierne, Tarpin, & Vernet, 1993:165.

*Species diagnosis.*—Gliding individuals may attain 20 cm in length and near 1.2 mm in diameter. Brain region red, body pink

anteriorly and yellowish white posteriorly, sometimes with a slight greyish tinge or blotching. Approximately seven small ocelli in roof of each cephalic fissure. Posterior end of cerebral organs some distance in front of buccal cavity. Some subepidermal glands penetrate into lateral rhynchocoelic blood lacunae (Fig. 6) and into lacunae dorsal and lateral to buccal cavity and initial esophagus. Ganglion layer of brain scattered into surrounding tissues, not enclosed in connective tissue. Sexual reproduction abortive, fissiparous. Contract by coiling.

No preoral excretory tissue was evident in any of the five specimens that were sectioned but a short segment was present to either side of the mouth (Fig. 6) with the efferent ducts exiting dorsally anterior to the esophagus. The nephric tubules of the rest of the system were of very small diameter and were often encased in subepidermal packet glands. They were not connected to the oral segments, and were first encountered some distance posteriorly but exited anterior to the esophageal/intestinal junction. Two lots of specimens were obtained about a year apart in an effort to resolve the peculiarities of this system. It was difficult to trace efferent ducts beyond the ICM, in part because of the large necks (Fig. 6) of the packet glands. All of the specimens may have belonged to a single clone and the peculiarities of the excretory system might be an abnormality. In some of the specimens there was a proliferation of mesenchyme cells obliterating the blood lacunae around parts of the foregut.

Gontcharoff (1951) considered the relationship of the posterior ends of the cerebral organs to the buccal cavity to warrant the separation of the species from *L. sanguineus*. Bierne (1993) utilized the color pattern of the adult antecerebral end as a character state distinguishing the subspecies *pseudolacteus* from *sanguineus*. They also noted that female *pseudolacteus* had never been collected.

*Myoisophagos lacteus* (Rathke, 1843), new combination
Figs. 1–4, 7

*Ramphogordius lacteus* Rathke, 1843:237.
*Nemertes lactea* Grube, 1855:151; Diesing, 1862:303; Czerniavsky, 1881:255.
*Borlasia lactea* Parfitt, 1867:215; McIntosh 1868, 1869.
*Lineus lacteus* McIntosh, 1873–1874:190. auctt.

*Species diagnosis.* — Gliding individuals may attain lengths in excess of 20 cm and 2 mm in diameter. Brain region red, body white to cream color. Ocelli may exceed seven in number on each side. Buccal cavity some distance behind posterior ends of cerebral organs. Some subepidermal glands penetrate into the two rhynchocoelic blood vessels and into the two dorsal blood lacunae above the buccal cavity, many abut the nerve plexus outside the inner circular muscles behind the mouth. Ganglion layer of brain enclosed with connective tissue. Excretory system with preoral segment on both sides. Gonochoric with pilidium larva. Contract by spiral coiling.

The distance between the buccal cavity and the cerebral organs, which is obvious in living animals, may be shortened by poor fixation procedures. The presence of excretory tubules in both lateral rhynchocoelic blood vessels and the penetration of the cell bodies of subepidermal glands (Fig. 3) into those vessels should alleviate any problems in identifying the species from serial sections.

Bierne et al. (1993) stated that "the five fissiparous *Lineus* species" shed eggs "directly in the sea water to develop into pilidium larvae." This has only been observed for *M. lacteus,* females being unknown in *M. pseudolacteus,* and the questionable comment by Coe (1889) re "*L. socialis*" is in total disagreement.

*Remarks.* — There is extensive literature dealing with this group of species, but most

of it is involved with fissioning, grafting, and regeneration. The heterograft studies of Bierne & Langlet (1974) clearly indicated genetic affinities of the species included in *Myoisophagos* in contrast to the disparate genetic implications of results with other *Lineus* species. Isozyme analyses by Alex Rogers (pers. comm.) support the separation of *Myoisophagos* from *Lineus* as well as the necessity for generic reassignment of *L. ruber* and *L. viridis.* The phylogenetic analysis by Bierne et al. (1993) utilized many of these characters but did not include morphological features. Their data lumped all of the fissiparous species including *L. pseudolacteus,* into a single species, *L. sanguineus,* and they erected three subspecies. Riser (1993) had concluded that all except the latter form constituted the species *L. sanguineus.*

The genus *Lineus* is characterized by the dorsal and ventral attachment of the rhynchodaeum dividing the cephalic blood lacuna into two lacunae which unite anterior to the rhynchodaeal pore, the presence of a thick layer of connective tissue separating the subepidermal gland layer from the OLM, the radial muscles forming a sling around the rhynchocoel but not continuing as a loop around the foregut, and the presence of a longitudinal muscle plate between the foregut and rhynchocoel. (The longitudinal muscle plate is initially interwoven with the bottom of the muscle sling that suspends the rhynchocoel from the dorsal wall of the body. These longitudinal muscles spread across the foregut postorally and extend between the bases of the subepithelial glands and the walls of the blood lacunae around the lateral esophageal wall almost to the level of the lateral nerve cords. They frequently occur among the bases of the glands in sections of contracted specimens.) These morphological features are not present in *Myoisophagos.* The subepithelial longitudinal esophageal muscles of *Myoisophagos* (Figs. 6, 11) continue beneath the intestinal cells for a short distance. Foregut rugae are rarely encountered dorsally in heteronemertines but usually are present laterally and ventrally where radial muscles insert among the epithelial cells of this portion of the gut (Fig. 11), facilitating dilation of the organ for ingestion of food, and producing sulci and rugae in the empty organ. Species of *Myoisophagos* are capable of ingesting food items more than twice the diameter of their bodies. *Tenuilineus* species are similar in dimensions to *Myoisophagos* but lack subepithelial esophageal longitudinal muscles and have a weakly developed radial musculature with very shallow sulci between small rugae and thus, the foregut is not capable of much expansion, nor of independent peristaltic waves to pass large particles into the hindgut. [The circular bands around the foregut of *Parborlasia corrugatus* (McIntosh, 1867), a species which can ingest very large food items, receive many fibers from the lateral and ventral radial muscles, producing a very thick layer which presses against the subepithelial glands but does not penetrate amongst them, however the dorsal radial muscles cross beneath the rhynchocoel as in *Myoisophagos.* The type specimens of *Mixolineus tauricus* Müller & Scripcariu, 1971 were retained by the authors and their present disposition is unknown. Their description differs from *Myoisophagos* in the absence of "splanchnic" muscles and the presence of an internal circular muscle layer in the proboscis. The role of radial fibers around the foregut is discussed and the reference to the absence of "splanchnische Muskulatur" appears to refer to the derivation of circular fibers from radial fibers. The figure of the cross section of the anterior proboscis Of *Mixolineus tauricus* is similar to that routinely encountered in *Myoisophagos* (Fig. 9) in which the thick endothelium can be mistaken for muscles especially where individual cells have been lifted off the longitudinal muscles.] Subepidermal mucus glands do not discharge at the apex of the head, and thus, frontal glands are absent. A few subepider-

mal mucus glands discharge laterally and ventrally around the proboscis pore (Fig. 7). The concentrated parenchymatous tissue of the precerebral region (Figs. 1, 2) sometimes included with the subepidermal glands as cephalic glands in heteronemertines extends ventrally almost to the brain but does not extend quite that far dorsally. Prenant (1922 Pl.V, fig. 2) referred to this tissue as supportive tissue consisting of "cellules vésiculeuse à mucus."

Moretto et al. (1976) noted the absence of a longitudinal muscle plate between the rhynchocoel and foregut, and the presence of the subepithelial longitudinal esophageal muscles, as characters that distinguish *M. sanguineus* and *M. lacteus* from *Lineus ruber* and *L. viridis*. The latter two species have an undivided blood lacuna arched over the rhynchodaeum, and lack a connective tissue layer separating the subepidermal glands from the OLM as noted by Riser (1993), and thus cannot be retained in the genus *Lineus*. Friedrich (1935) established the genus *Heterolineus* and against the rules of nomenclature, designated *Lineus longissimus*, the type species of the genus *Lineus*, as the type species of his new genus. Cantell (1976) noted without comment that the basic morphology of *Heterolineus longissimus* Friedrich, 1935 differed radically from that of *Lineus longissimus* (Gunnerus, 1770). *Heterolineus* may be a valid genus but the type species must be rediscovered and adequately described. Neither species assigned to it can be placed in *Myoisophagos*.

## Acknowledgments

## Literature Cited

Bürger, O. 1892. Zur Systematik der Nemertinenfauna des Golfs von Neapel.—Nachrichten von der Königliche Gesellschaft der Wissenschaften 5:137–178.

———. 1897–1907. Nemertini (Schnurwürmer). *In* H. G. Bronn, ed., Klassen und Ordnungen des Tierreichs, Supplement, 4:452 pp.

Bierne, J. 1983. Nemertina. Pp. 147–167 *in* K. G. Adiyodi and R. G. Adiyodi, eds., Reproductive biology of invertebrates. Vol. 1: oogenesis, oviposition, and oosorption. John Wiley & Sons, New York, 770 pp.

Bierne, J., & C. Langlet. 1974. Recherches sur l'immunité de greffe chez les Némertiens du genre *Lineus*. Etude de la réponse primaire à la transplantation hétérospécifique.—Comptes Rendus des séances de l'Académie des Sciences, Paris 278:1445–1447.

———, M. Tarpin, & G. Vernet. 1993. A reassessment of the systematics and a proposal for the phylogeny of some cosmopolitan *Lineus* species (Nemertinea).—Hydrobiologia 266:159–168.

Cantell, C.-E. 1976. Complementary description of the morphology of *Lineus longissimus* (Gunnerus 1770) with some remarks on the cutis layer in heteronemertines.—Zoologica Scripta 5:117–120.

Coe, W. R. 1899. Notes on the times of breeding of some common New England nemerteans.—Science 9:167–169.

———. 1931. A new species of nemertean (*Lineus vegetus*) with asexual reproduction.—Zoologischer Anzeiger 94:54–60.

———. 1943. Biology of the nemerteans of the Atlantic coast of North America.—Transactions of the Connecticut Academy of Arts and Sciences 35:129–328.

———. 1951. The nemertean fauna of the Gulf of Mexico. *In* Gulf of Mexico its origin, waters, and marine life.—Fishery Bulletin U.S. Fish and Wildlife Service 89:303–309.

Corrêa, D. D. 1956. Estudo de Nemertinos Mediterrâneos (Palaeo e Heteronemertini).—Anais da Academia Brasileira de Ciências 28:195–214.

———. 1961. Nemerteans from Florida and Virgin Islands.—Bulletin of Marine Science of the Gulf and Caribbean 11:1–44.

Czerniavsky, W. 1881. Materialia ad zoographiam Ponticam comparatum. Fasc. 3 Vermes.—Bulletin de la Société des Naturalistes de Moscou 55:239–260.

Diesing, K. M. 1862. Revision der Turbellarien. Abteilung Rhabdocoelen.—Sitzungsberichte der Akademie der Wissenschaften in Wien. Abt. 1. 46:246–307.

Friedrich, H. 1935. Studien zur Morphologie, Systematik und Ökologie der Nemertinen der Kieler Bucht.—Archiv für Naturgeschichte 4:293–375.

Gibson, R. 1982. Nemertea. Pp. 823–846 *in* S. P. Parker, ed., Synopsis and classification of living organisms. McGraw-Hill, New York.

Gontcharoff, M. 1951. Biologie de la régénération et

de la reproduction chez quelques Lineidae de France.—Annales des Sciences Naturelles, Zoologie s.11, 13:151–235.

Grube, E. 1855. Bemerkungen über einige Helminthen und Meerwürmer.—Archiv für Naturgeschichte 21:137–158.

Isler, E. 1901. Unpublished Inaugural-Dissertation, Basel, 53 pp.

———. 1902. Die Nemertinen der Sammlung Plate.—Zoologische Jahrbücher, Suppl. 5:273–280.

Leidy, J. 1855. Marine invertebrate fauna of Point Judith, R. I., and New Jersey.—Journal of the Academy of Natural Sciences of Philadelphia s. 2. 3:134–151.

McIntosh, W. C. 1867. On the gregariniform parasite of *Borlasia.*—Transactions of the Royal Microscopical Society of London, N.S. 15:38–41.

———. 1869. On the structure of the British nemerteans, and some new British annelids.—Transactions of the Royal Society of Edinburgh 25: 305–433.

———. 1873–1874. A monograph of the British Annelids. (part 1) The Nemerteans.—Ray Society London 22:1–218.

Monastero, S. 1930. I Nemertini della spiaggia di Palermo.—Atti della R. Accademia di Scienze, Lettere e Belle arti di Palermo 16:3–24.

Moretto, J. A., G. Vernet, & M. Gontcharoff. 1976. Aspects anatomo-histologiques de quelques Lineidae (Hétéronémertes).—Bulletin de la Société Zoologique de France 101:221–230.

Müller, G. I., & D. Scripcariu. 1971. *Mixolineus tauricus* n.g. n.sp. und weitere beiträge zur kenntnis der Nemertinen des Schwatzen Meeres.—Cercetari Marine 2:5–25.

Nusbaum, J., & M. Oxner. 1910a. Beiträge zur Kenntnis der Regenerationserscheinungen bei der Nemertinen.—Bulletin International de L'Académie des Sciences de Cracovie. s. B: Sciences Naturelles 3:1–16.

———, & ———. 1910b. Studien über die Regeneration der Nemertinen. 1. Regeneration bei *Lineus ruber* (Müll.).—Archiv für Entwicklungsmechanik der Organismen 30:74–132.

Oudemans, A. C. 1885. The circulatory and nephridial apparatus of Nemertea.—Quarterly Journal of Microscopical Science. Supplement, N.S. 25: 1–80.

Oxner, M. 1909. Sur deux modes différents de régénération chez *Lineus ruber.*—Comptes rendus des séances de l'Académie des Sciences, Paris 148:1424–1426.

———. 1910. Études sur la régénération chez les Némertiens. 1. La Régénération chez "*Lineus ruber*" (Müll).—Introduction: Observations biologique.—Annales de L'Institut Océanographique 1, 8:1–32.

Parfitt, E. 1867. A catalogue of the annelids of Devonshire, with notes and observations.—Transactions of the Devonshire Association for the Advancement of Science 2:209–246.

Prenant, M. 1922. Recherches sur le parenchyme des Plathelminthes.—Archives de Morphologie Générale et Expérimentale 5:1–174.

Rathke, H. 1843. Beiträge zur Fauna Nowegens.—Nova Acta Akademie Leopoldina Naturae Curios 20:231–237.

Rathke, J. 1799. Jagttagelser henhörende til Indvoldeormenes og Blöddyrenes Naturhistorie.—Skrivter af Naturhistorie Selskabet Kjöbenhavn 5:83–84.

Riser, N. W. 1988. *Notogaeanemertes folzae* gen. n. sp. n., an additional ecologically restricted hoplonemertean from New Zealand.—Hydrobiologia 156:125–133.

———. 1993. Observations on the morphology of some North American nemertines with consequent taxonomic changes and a reassessment of the architectonics of the phylum.—Hydrobiologia 266:141–157.

Vernet, G. 1983. The body wall pigment of the nemertean *Lineus sanguineus*: a morphological study.—Cytobios 36:197–200.

———, & J. Bierne. 1983. Étude de la couleur du corps de trois némertes (*Lineus sanguineus, L. pseudolacteus et L. lacteus*): application au marquage des tissus des chimèrus interspécifiques.—Bulletin de la Société Zoologique de France 108:257–266.

Verrill, A. E. 1873. Report upon the invertebrate animals of Vineyard Sound and the adjacent waters, with an account of the physical characters of the region.—Report of the United States Commissioner of Fisheries for 1871–1872:295–852.

———. 1892. The marine nemerteans of New England and adjacent waters.—Transactions Connecticut Academy of Arts & Sciences 8:382–456.

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